SPONGE SCIENCE, FROM ORIGIN TO OUTLOOK

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Much of the important data, and most of the progress made on sponge biology has come from careful *in vivo* and *in vitro* studies on living populations. These techniques were used in studies conducted over a century ago, but much of this early work has been overlooked, or distorted during its transmission to the present time. This review revisits the scientific philosophy and techniques of our predecessors. It evaluates the quality of their observations, experimental prowess and originality in thought, and highlights the pivotal discoveries that have produced our present concept of 'what is a sponge', underlining those fields of study, such as developmental biology, where information is incomplete or lacking altogether. ☐ *Porifera, historical review, sponge biology, animality.*

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In 1948, as I began my career in science, I asked some of my mentors in sponge biology, Emile Topsent, Odette Tuzet, Henriette Meewis and Paul Brien, whether or not working on sponges, particularly their developmental biology, was still a worthwhile pursuit for a young scientist. Now, 50 years later, despite the tremendous progress we have made in our understanding of the general and molecular biology of sponges, it is clear to me that we need much more work to better understand development, growth and morphogenesis of sponges.

Scientific knowledge is a human collective and diachronic phenomenon, with each of us adding our own observations, thoughts and experiences (sometimes orally transmitted, but mostly in written form and as artwork), to the accumulated body of information from the past. Reading ancient documents is often amusing for their apparent naive contents, but often the answer is not obvious without many years of experimentation and observation. Moreover, is the answer definitive?

For this plenary address on the 'Origin & Outlook' of sponge biology, it is necessary to revisit the scientific philosophy and techniques available to our predecessors, in order to evaluate the quality of their observations, their experimental prowess and originality of thought. Indeed, personal reading of the older literature is invaluable; one can discover observations which have been forgotten or distorted by their transmission and subsequent interpretation, and one can also find hypotheses which more contemporary experiments subsequently invalidated or confirmed. It is essential to read original documents in order to better understand the great debates on 'animality', individuality, diblasty and inversion of layers, origin of the phylum, origin of bathyal and abyssal fauna, cellular differentiation and re-differentiation, internal transmission of information within this multicellular organism, self-not-self recognition, and so forth.

Studying living populations of marine animals is difficult at best, but unequivocally *in vivo* and *in vitro* observations on sponges over the centuries have contributed most to what we know about the phylum today. It was no accident that sponge science began somewhere in the eastern Mediterranean during an earlier millenium, in the province of sponge fishers, subsequently reaching the western Mediterranean, then the French coasts, and then the British Isles at the end of the 18th century. Discoveries made from field observations have had a substantial influence on our collective thinking about the Porifera, and in some cases these discoveries have changed our perception of the phylum completely.

Two such extraordinary events have occurred since the previous conference (4th International Porifera Congress, University of Amsterdam, 1993), both widely reported by the international media: 1) the existence of carnivorous sponges with neither aquiferous system nor choanocytes (Vacelet & Boury-Esnault, 1995); and 2) the presence of soft sponge elements and embryos in southern Chinese Guizhou deposits some 580 million years old (Chia-Wei Li, Ju-Yuan Chen, Tzu-En Hua, 1998). Both these discoveries have made us re-evaluate two key aspects of sponge structure and biology: the interaction between, and the respective functions of, flagellated cells and amoebocytes.

First, Jean Vacelet and Nicole Boury-Esnault (1995) found that *Asbestopluma* lacked choanocytes yet it could breath, eat, and reproduce successfully. They found that *Asbestopluma* uses microscleres embedded along long filaments that are supported by long, aligned megascleres to actively capture the prey; the prey is enveloped and ingested by epithelial cells on the filaments. This system of macrophagy replaces the microphagous suspension-feeding by choanocytes, unique to the Porifera. Typically, the development of the aquiferous system and differentiation of choanocytes are the final ontogenetic events in sponge development. From the pioneering work of H.V. Wilson (1932) we know that choanocytes and canals may disappear from a severely distressed sponge (termed involution bodies, resting bodies or reconstitution diamorphy). Similarly, we also know from the pioneering work of J.S. Huxley (1911), that involution bodies in Calcarea are clearly made of archeo-amoebocytes that lack basal bodies. Perhaps early sponges did not require an aquiferous system?

The characteristic synapomorphy of the Porifera is the possession of an aquiferous system and choanocytes, yet this appears to be the most labile part of a sponge. By trying to understand how the aquiferous system is formed and reformed during morphogenesis, can we hope to approach the phylogenetic origin of sponges ? J.S. Huxley (1911) thought not, yet carnivorous sponges live and survive perfectly well without this characteristic synapomorphy of the phylum. It would be of great interest to know whether there is a transitional aquiferous system present during growth and development of *Asbestopluma*. Is *Asbestopluma* some kind of permanent diamorphy?

The second discovery, of ancient Guizhou sponges by Chia-Wei Li, Ju-Yuan Chen and Tzu-En Hua (1998), suggests that larval flagellated cells and amoebocytes were already present in sponges as old as 580MY. Does this mean that modern species do not differ substantially from those early in the evolution of the group ? How much further does the group extend into the past?

To understand these contemporary viewpoints in the correct context, it is informative to review early historical interpretations of the structure of the aquiferous system and the anatomy of the soft parts of a sponge before modern histological techniques and descriptive embryology provided us with our current understanding of sponge morphogenesis.

At the end of the 18th century Peter Pallas (1766) and John Ellis (1755, 1786) suggested that sponges were of animal nature, contrary to popular opinion in those times. Debates on the 'animality' of sponges continued for at least a century.

Animality, as understood in those times, was assigned to organisms which were capable of voluntary movement, muscular response, and were sentient. Observers sought evidence of responsiveness and of motion, which would be similar to muscular contraction, for sponges (which by nature are a fixed animal). Some investigators, like Donati (1750), observed that the contact between any object and the sponge caused the sponge to contract, whereas others found no such response. In the absence of any sensory reaction or of motion by the sponge, some philosophers suggested they could detect animality based on the nature of the smell arising during sponge decomposition: this smell depends, after all, on the 'animal' chemical structure or pattern of the organism. This approach is complicated by the fact that most naturalists at that time were only familiar with very few marine sponges (at that time assigned to the greatly misused genera *Spongia*, '*Alcyonium*' and *Tethya*), in some cases only one species, or they worked exclusively on freshwater sponges. Freshwater spongillids are typically green when alive, which led observers to think they were plants.

Convergence of viewpoints on the nature of sponges gradually emerged, especially following the works of Grant (1825-26), Dutrochet (1828), Dujardin (1838) and Laurent (1844) on freshwater and marine sponges. Prior to these authors' works it was clear to the casual observer that the sponge surface was perforated. This feature was the most consistent amongst the known species of sponges, which eventually led to the phylum being named Porifera (pore-bearing) by Robert Grant (1836). But few authors had any idea on the nature of these pores. Were they normal apertures produced by the sponges or were they caused by foreign organisms, such as worms or polyps,

P.S. PALLAS 1766

Animal ambiguum, crescens, torpidissimum. Stirps polymorpha, e fibris contexta, gelatina viva obvestitis. Oscula oscillantia, seu cavernae cellulae ve superficiei

C.v. LINNE 1767

Flores. Foraminibus respirant aquam. Stirps radicata, pilis contexta, flexilis bibula

J.ELLIS 1786

Animal fixum, flexile, polymorphum, torpidissimum, contextum vel e fibris reticulatis, vel e spinulis, gelatina viva vestitis, osculis seu foraminibus superficiei aquam respirans.

FIG. 1. Definitions of a sponge from the earliest literature: Pallas (1766), Linneaus (1767), Ellis & Solander (1786).

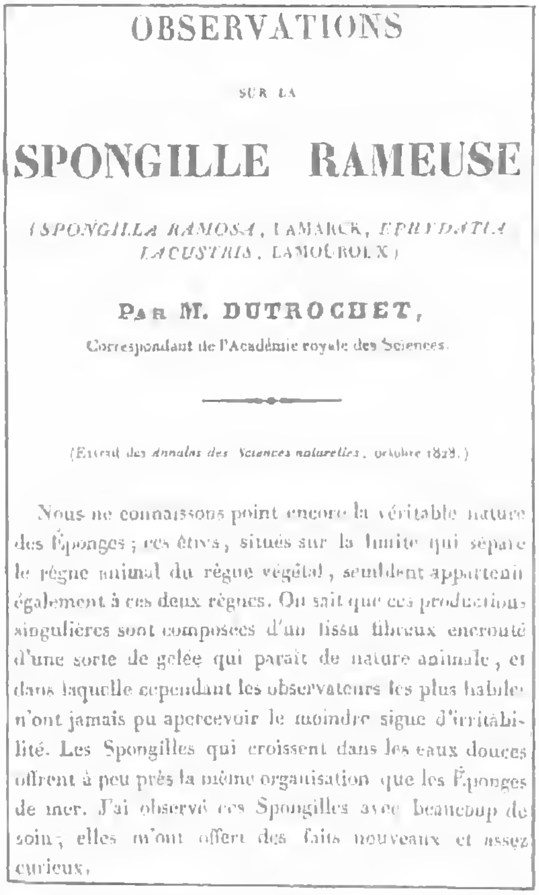
burrowing into the sponge? Many, including Jean Baptiste Monet de Lamarck (1814-16), favoured the latter hypothesis. In fact Lamarck's (1814) classification of the Zoophytes was centred on the presence or absence of polyps: with sponges included in the latter group, and defined as Polypiers empâtés — made of a common substance and ... without polyps.

Those who observe a living sponge, however, immediately realise that the pores are an integral part of the sponge anatomy, conducting water flow into and out of the body. Some authors, such as Marsigli (1711) and Ellis (1755), imagined (probably moreso than they actually observed), a double flow into and out of the same pore — a systolic-diastolic phenomenon. Others, like Grant (1825) and Dutrochet (1828), observed a unidirectional, continuous water flow exiting the sponge at constant speed. But, they wondered, if water keeps flowing out of the sponge, where and how does it go in?

Dutrochet (1828) was convinced that the freshwater spongillid was a plant. He perceived that it was green, it formed a membranous extension that grew through expansion at its edges, like the algae *Ulva*, it didn't appear to have food cavities and therefore it probably fed by absorbing solutions of water enriched with nutrients, much like a plant. To him it was a plant whose chemical structure was identical to some extent to that of animal tissues. However, Dutrochet observed cavities in sponges with a transparent membrane covering them. He noted that this membrane also covered the entire external surface; it was not sensitive when touched by a foreign object; and it was capable of creating a conical protuberance (oscules) capable of continuously expelling water through the apical part. Dutrochet dismissed the hypothesis that water was expelled from the sponge by commensal Crustacea, and instead he proposed that water was expelled from *Spongilla* via 'some kind of a force' produced by the living animal itself. He did not, however, discover the inhalant pores, but he hypothesised instead that water was drawn slowly into the sponge by adsorption over the whole surface. According to his theory, the expulsion of water from the sponge depended on endosmosis, with the continuous introduction of surrounding water into the cavities of *Spongilla*, which he said were filled with a denser organic fluid.

Grant (1825-26) was also sure that sponges were animals. To him it was obvious that sponges had two types of orifices: 1) larger faecal orifices, through which water was forcefully expelled; and 2) numerous smaller pores through which water entered. Grant, who studied living populations of several sponge species in coastal Scotland, observed a continuous water circulation flowing through many internal canals. Although he was unable to suggest what the 'motor' was that drove this circulation, he was none-the-less certain that something like this existed. In fact he commented that minuscule bodies, or granules, organised along the canals might be directly involved, and that water flow is similar to that which might possibly be generated via a flagellar system. Demonstrating remarkably modern vision Grant was sure that water current was one of the vital functions of the pore-bearing animal, and that it helped the animal to feed, breath and even reproduce.

In addition to the aquiferous system Grant also noted the sponge soft parts were differentiated into a general cellular substance and a body of material unifying the spicules. This cellular substance, he wrote, twenty years before the cell-theory was proposed by Virchow and others,



OBSERVATIONS

SUR LA

SPONGILLE RAMEUSE

(*SPONGILLA RAMOSA*, LAMARCK, *EPHYDATIA LACUSTRIS*, LAMOUROUX)

PAR M. DUTROCHET,

Correspondant de l'Académie royale des Sciences.

(Extrait des *Annales des Sciences naturelles*, octobre 1828.)

Nous ne connaissons point encore la véritable nature des Éponges; ces êtres, situés sur la limite qui sépare le règne animal du règne végétal, semblent appartenir également à ces deux règnes. On sait que ces productions singulières sont composées d'un tissu fibreux encroûté d'une sorte de gelée qui paraît de nature animale, et dans laquelle cependant les observateurs les plus habiles n'ont jamais pu apercevoir le moindre signe d'irritabilité. Les Spongilles qui croissent dans les eaux douces offrent à peu près la même organisation que les Éponges de mer. J'ai observé ces Spongilles avec beaucoup de soin; elles m'ont offert des faits nouveaux et assez curieux.

FIG. 2. Definition of a sponge, from Dutrochet (1828).

was mostly located in the spaces between the walls of internal canals, and appeared to be most obvious during the reproductive period of the sponge.

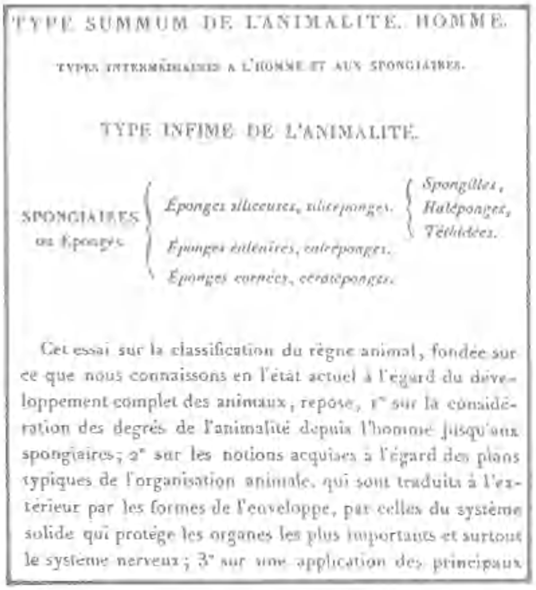
Dutrochet (1828) was the first to explain shape changes of sponges through cellular movements. He focused on the transparent membrane and membranous ducts which provided a pathway for the continuous flow of water out of the sponge. Through regular observations he noticed that these ducts changed shape and length, stretching and shrinking periodically. He suggested these movements were not the result of sensitivity but a mechanism for transporting substances from one part of the tube to another. To him the membranes were made of vesicular globules, and changes to their shape and length were caused by the transport of elementary globules. These globules were not static but moved over each other without detaching, in a predefined direction, using a kind of sliding motion. Changes in shape and movement were too slow to be visually observed, much like the hands of a clock, but shape changes could be seen over time. 'This fact is physiologically of the highest importance' stated Dutrochet, 'It is a new vital action which plays one of the main roles in stretching the plant's size, the immediate agent responsible for the vital motion uncovered in its very nature and action mode'.

Felix Dujardin (1838) was well known for his studies on Rhizopods and Amoebae, in which he had observed very slow, micrometrical movements. He began studies on sponges during 1835-1837, working on *Cliona celata*, *Halichondria*, *Halisarca* and *Spongilla* species, to try and understand sponge organization. From these studies he observed irregular globules made of a contractile substance which, when drawn 20 times at 5 minute intervals, gave 20 different profiles. These globules periodically generated round expansions and thin appendages, much like shape changes to amoebae. He subsequently demonstrated the animal nature of sponges before the French Academy of Sciences, based on the presence of these contractile expansions and by the crawling motion of these 'packets'. Moreover, in a *Spongilla* from the Seine River in Paris, Dujardin also saw packets with flagellated filaments which he said 'determined the water flow and streams in the oscules'.

Dujardin and Dutrochet were clearly at odds, and before the French Academy, Dujardin stated 'Mr Dutrochet, who refuses to admit sponge contractility, explains all their shape changes by the motion of molecules, probably vesicular according to him, which make up the tissues of external membrane'. This controversy was further complicated by the ambiguity of the words contractility, motion and movement, mandatory to the concept of animality.

Whereas Dutrochet was the first to describe shape changes of the sponge caused by directed cell motion, and also showed the importance of the external pinacoderm, Dujardin described for the first time the presence of amoebocytes with pseudopodial extensions. In 1844 Jean Laurent suggested that the presence of this external membrane was the sign of the beginning of life for a perfect state of *Spongilla* species. In that same year Laurent published this classification, which has been completely forgotten today.

These early, careful, time-lapse ocular observations of Dutrochet and Dujardin demonstrated that the sponge and its constituents were able to



TYPE SUMMUM DE L'ANIMALITE. HOMME.

TYPES INTERMÉDIAIRES A L'HOMME ET AUX SPONGIAIRES.

TYPE INFIME DE L'ANIMALITE.

SPONGIAIRES ou Éponges.
Éponges siliceuses, silicéponges. Spongilles, Haléponges, Téthidées.
Éponges calcaires, calcéponges.
Éponges cornées, cératéponges.

Cet essai sur la classification du règne animal, fondée sur ce que nous connaissons en l'état actuel à l'égard du développement complet des animaux, repose, 1° sur la considération des degrés de l'animalité depuis l'homme jusqu'aux spongiaires; 2° sur les notions acquises à l'égard des plans typiques de l'organisation animale, qui sont traduits à l'extérieur par les formes de l'enveloppe, par celles du système solide qui protége les organes les plus importans et surtout le système nerveux; 3° sur une application des principaux

FIG. 3. Succinct classification of the animal kingdom, from Laurent (1844).

move and displace, although the speed of these phenomena was visually undetectable. A century later, using time-lapse cinematography, Ankel (1965) studied cellular motion of spongillid fragments sandwiched between two glass-slides. Subsequently, Efremova (1967), Pavans de Ceccatty (1979), Rasmont (1975) and their teams produced a wealth of fascinating observations on cell motility. For Pavans de Ceccatty, who essentially focused on information transfer systems and integration, cell mobility and displacement were basic features of sponge organisation. For Rasmont, who was more interested in experimental morphogenesis, the most striking characteristic to him was the extreme mobility of all sponge constituents. For example, using a frame-by-frame analysis he concluded that the movement of spongillid amoeboid cells during gemmulation could be statistically tested for random versus directed movement.

It is strange though, that although there has been so much research on embryology, postlarval, postgemmular and postdiamorphic development, we still have so little data on growth and true morphogenesis (i.e. shape achievement), a character so important to the taxonomist but still largely speculative.

We have some good models, such as *Leucosolenia*, whose growth has been thoroughly studied by W. Clifford Jones (1964, 1965), and particularly from work on the spongillids — a group intensively studied since the beginning of sponge science (e.g. Grant, Dutrochet, Dujardin, Laurent, Ankel, Rasmont, van de Vyver and many others). Nevertheless, there are many questions still unanswered. In particular, we know little about intercellular events and chronology during the simultaneous organisation of the skeleton and the aquiferous system (so different in the three classes of Porifera); the role of primary external physical factors, such as light and hydrodynamics, in triggering, orienting and maintenance of cell movements; the regulatory processes influencing the relative proportions of cell populations and the local conditions prevailing during their differentiation; the movements of sclerocytes and factors that determine which types of megascleres are produced, where they are localised and distributed within the skeleton (such as in prismatic or cubic meshes, isotropic prismatic system, or in ascending dendritic fibres), and the consequences of their localisation within the sponge.

More than a century after Grant, I also spent a great deal of time observing the littoral sponge fauna around Roscoff, including the same species studied by Grant. My curiosity led me to follow the shape changes that sponges undergo over many years. I noted that fragmentation of individual specimens was frequent, as was the susequent fusion of these same sponge fragments. It was clear that fragmentation was not only produced by catastrophic events, such as storms or predation, but also occurred as a much more gradual process, presumably linked to adaptation of the sponge to local environmental conditions. Sometimes these processes can be observed in the aquarium, and sometimes it is possible to generate them experimentally. Slow fragmentation is the result of massive cellular movements, which are not very different from those described by Dutrochet in *Spongilla*. Both fragmentation and fusion are opposite and complementary and are 'the two fundamental tendencies of the sponge to concentrate and to isolate from the external environment', as stated by Borojevic (1971) and Wilson (1932) before him. Through the manipulation of light and water circulation it is possible to generate the partial or complete motion of the sponge, whose cells are able to move and leave the existing skeleton to build another in a more physiologically favourable environment. Ankel (1965), Ankel & R. Eigenbrodt (1950) and Rasmont (1975, 1979) provided pivotal data on these processes.

What other organisms are easily able to get rid of their skeleton? This phenomenon is unthinkable in more mobile organisms, and certainly does not occur within the plants, and is perhaps unique amongst the Porifera. Of course, morphological freedom associated with cellular migration has constraints and genetic limitations; but why is shape more stable in some species despite their constant local morphological readjustments? Even *Tethya*, a sponge universally characterised by it 'golf ball' shape, can distort and move. In a compact spherical sponge that lacks cavities and has a severely localised aquiferous system, an internal equilibrium is set up between cell populations which are using internal energy stocks. Growth under cell proliferation requires an increase in exchange between external and internal surfaces. Growth of the exchange zone occurs through folding or multiplication of choanocyte chambers, and by regulating inhalant cavities. Growth of the external surface can be horizontal, polyaxial and peripheral, or, vertical, monaxial and apical, and all intermediate situations exist between the prolate and oblate states.

Recently, Jaap Kandoorp (1995) described a new fractal approach to *Haliclona* morphology, which in the future should be coupled to 3-dimensional analyses of the aquiferous system, following the method of corrosion casts developed by Bavestrello et al. (1988). But we also have to investigate the signals which determine the orientation of migrating cells, and we have to know the control mechanisms that determine the motile behaviour of cells of this 'torpidissimum' animal.

We enter a new millenium with new and fantastic technology. Widespread use by researchers and increasing speed of nucleic acids sequencing technology, together with computerised analysis of sequences, provides more and more information on the genetic make up of sponges, and at this rate it might be reasonable to hope that by the next century we will know the complete sponge genome, a current witness of a primitive multicellular organism. It will be the result of teamwork which has to be carefully organised and planned. The choice of the reference model species could well be *Ephydatia fluviatilis*. But not everything will be explained by knowing all about the genes, although certainly it is a mandatory step. Progress in developmental biology, one of the most important scientific fields of the next century, shows that the chronology of gene expression (also an essential subject), does not yet explain the topological evolution of the blastula, a primarily spherical organism, towards increasingly complex stages possessing multiple compartments and under the constant influence of environmental factors. It be equally necessary to direct team efforts to the central theme of growth and form, following the trail pioneered such a long time ago by d'Arcy Thomson (1917).

As Grant wrote, 'This animal affords many curious and interesting subjects of inquiry to those who [like John Hooper] have leisure and opportunities of examining the more perfect species of tropical seas. Though probably the simplest of animal organisation, the investigation of its living habits, its structure and vital phenomena, and the distinguishing characters of its innumerable polymorphous species is peculiarly calculated to illuminate the most obscure part of Zoology, to exercise and investigate our intellectual and physical powers, and to gratify the mind with the discovery of new scenes of infinite wisdom in the economy of Nature'.

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